

A QUANTITATIVE REVIEW OF THE HORSE *EQUUS* FROM SOUTH AMERICA

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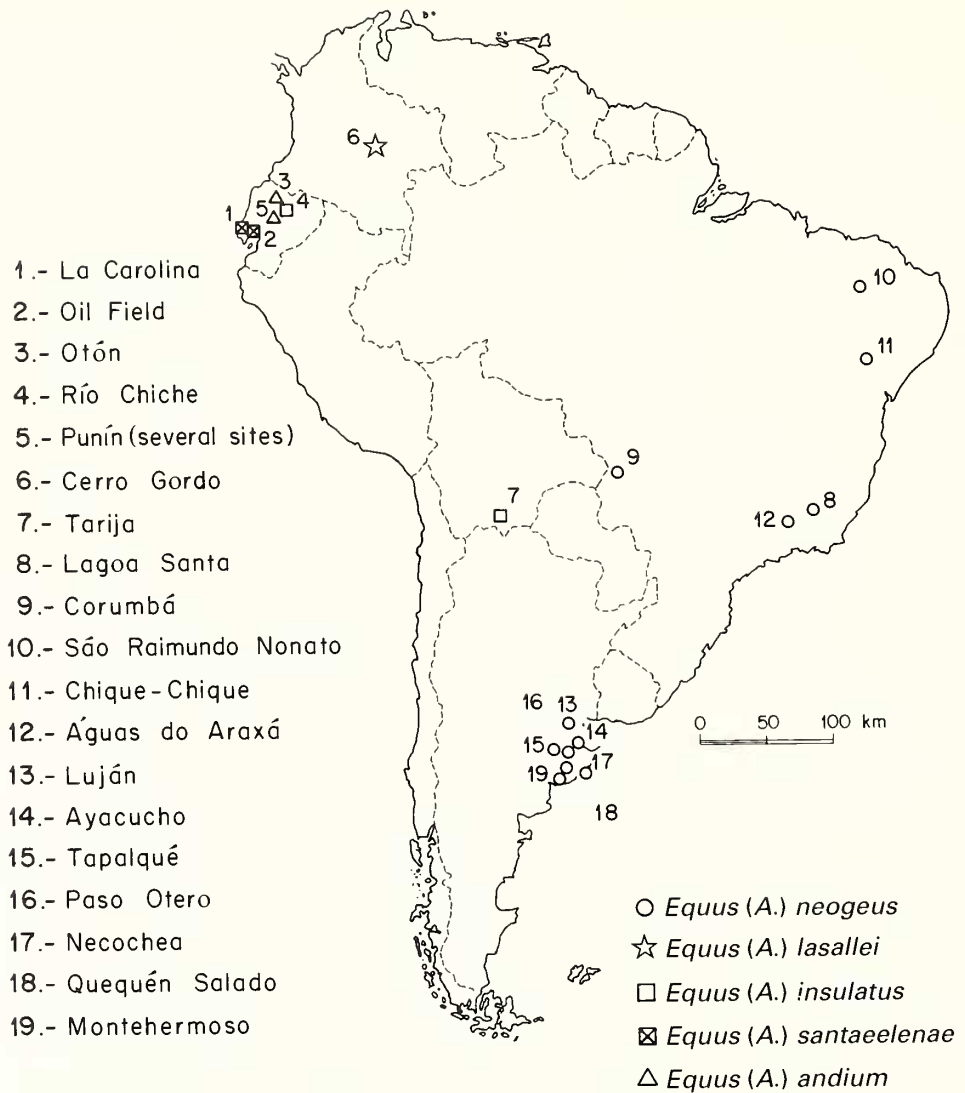
ABSTRACT. The species of *Equus* (*Amerhippus*) are revised using multivariate analysis of dental and autopodial remains, and some morphological characters of the skull and dentition. We recognize five species: *E. (A.) andium*, *insulatus*, *neogenus*, *santaeelenae*, and *lasallei*. They have been recorded in Argentina, Bolivia, Brazil, Colombia and Ecuador, through the Middle and Upper Pleistocene. They show peculiar adaptive features in the distal part of the extremities as a response to different environmental conditions.

THE Quaternary equid record from South America is very rich. From a palaeobiogeographic point of view, the remains are distributed throughout the continent, from Ecuador to central Argentina. There are very important quantitative and qualitative collections representing all parts of the skeleton of all species.

Equus arrived in South America after the Great American Biotic Interchange (Webb 1976). From Lund (1840) to the present, numerous records and new species have been attributed to this genus. Sefve (1912), and Boule and Thevenin (1920) have studied South American *Equus* in monographic works. Hoffstetter (1952), in his review of Ecuadorian mammals, recognized only six species of this genus, all included in the subgenus *Amerhippus* Hoffstetter, 1950. He also included in this South American subgenus, one North American species *Equus occidentalis*. Porta (1960) described a new species collected by Brother Daniel, *Equus lasallei*, from the Late Pleistocene of Colombia. More recently, MacFadden and Azzaroli (1987) discussed the status of the species cited by Hoffstetter (1952) and recognized as valid species: *E. andium*, *E. lasallei*, *E. insulatus* and possibly *E. curvidens*, without a clear definition of the others (*E. santaeelenae*, *E. martinei*, *E. neogenus*). Azzaroli (1992) provisionally recognized eight valid species from South America (*Equus curvidens*, *E. andium*, *E. insulatus*, *E. haasei*, *E. martinei*, *E. santaeelenae* and *E. lasallei*, and the poorly known *E. neogenus* with doubts), all ascribed to the subgenus *Amerhippus*. He also included in this group two North American species: *E. fraternus* and *E. conversidens*.

The subgenus *Amerhippus* is recorded in South America from the Middle Pleistocene (Ensenadan Land Mammal Age), appearing after the genus *Hippidion*, which was first recorded from the Late Pliocene in that continent. That group of horses is more evolved than *Hippidion* which has some primitive characters (Alberdi and Prado 1992, 1993). Species of *Amerhippus* show two different morphological patterns; one of them corresponds to forms adapted to grasslands and open habitats, and the other to mountain forms. Each group is quite homogeneous, with little variation in size throughout its geographical and stratigraphical distribution. This point has not been given sufficient consideration in previous taxonomic reviews, which describe large numbers of species.

The aims of this study are: (a) to identify the groups of *Equus* (*Amerhippus*) resulting from multivariate analysis of the upper and lower dentitions, metacarpals (MCIII), calcaneum (CA), astragalus (AS), metatarsals (MTIII) and first phalanges of the third digit (1FALIII); (b) to determine which morphometric characteristics and bones allow the best identification of the different species; (c) to redefine the generic and specific diagnoses of South American horses, and (d) to establish valid taxonomic names.



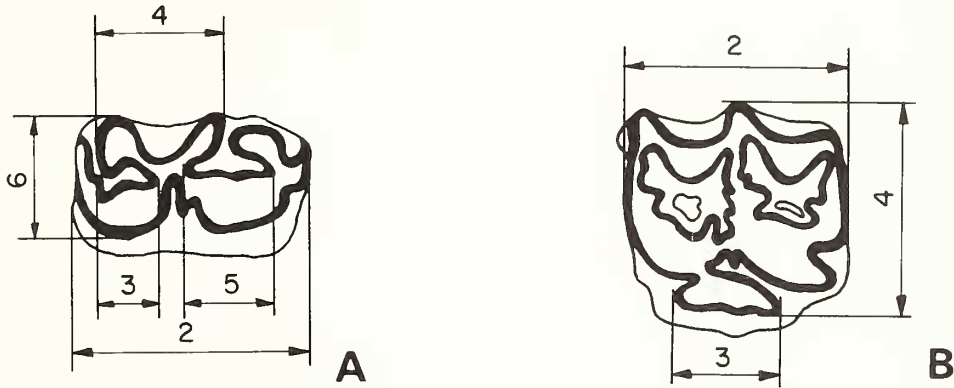
TEXT-FIG. 1. Geographic distribution of *Equus (Amerhippus)* localities.

MATERIAL AND METHODS

The studied material includes the material studied by Hoffstetter (1952) and Boule and Thevenin (1920), in the Museo de la Escuela Politécnica Nacional of Quito, Ecuador (MEPN), Institut de Paléontologie du Muséum National d'Histoire Naturelle of Paris, France (IPMNH) and Museo Nacional de Historia Natural (MNHN) and GEOBOL, La Paz, Bolivia. In addition, the following collections were examined: in Argentina: Museo de La Plata (MLP), Museo de Ciencias Naturales 'Bernardino Rivadavia' of Buenos Aires (MACN), Museo Municipal de Ciencias Naturales 'L. Scaglia' of Mar del Plata (MMCN), Museo de Historia y Tradición of Lobería (MHTL), Instituto Miguel Lillo of National University of Tucuman (IML); in Colombia: Museo de Ciencias of Lasalle University (MCLU) and National University of Bogotá (NUB); in USA, Frick Collection of the American Museum of Natural History of New York (AMNH); and in England, The Natural History Museum, London (BMNH).

Several South American specimens lack a precise stratigraphical location because they come from very old collections where the stratigraphy is rarely indicated. Specimens analysed here come from the following sites: Tarija (Bolivia), considered Middle Pleistocene (MacFadden *et al.* 1983) (7 in Text-fig. 1); La Carolina and Salinas Oil Fields in Santa Elena Peninsula (1 and 2 in Text-fig. 1), several localities in the Ecuadorian Andes (3 and 5 in Text-fig. 1) and Rio Chiche (4 in Text-fig. 1). The Santa Elena sites are assigned to Pichilingue Formation by ^{14}C about 26000 ± 100 BP (Baldock 1982), the Ecuadorian Andes localities (Chalán, Alangasí, El Colegio, Q. Colorada, Otón, Q. Grande, etc), are placed between 40000 and 4000 years BP by Dugas (1986). The Rio Chiche site is considered to be older than the others (Hoffstetter 1952), and all localities from Brazil (8 to 12 in Text-fig. 1) and Buenos Aires province (13 to 19 in Text-fig. 1) are considered to be latest Pleistocene (Cunha 1971, 1981; Paula Couto 1979; Tonni *et al.* 1985; Bargo *et al.* 1986; Prado *et al.* 1987; Alberdi *et al.* 1989; Guérin 1991; Carbonari *et al.* 1992). Finally, Cerrogordo in the Bogotá savanna (Colombia) is referred to the late Pleistocene by Porta 1960 (6 in Text-fig. 1).

The upper and lower dental rows, MCIII, CA, AS, MTIII and 1FALIII from each locality or group of localities are considered as a single Operational Taxonomic Unit (OTU). The morphometric characters used in the analyses are after Eisenmann *et al.* 1988 (see Text-figs 2–4, and



TEXT-FIG. 2. The measurements of the occlusal view of the lower and upper cheek teeth. A, lower; 2, occlusal length; 3, length of the prefixid; 4, length of the double knot; 5, length of the postflexid; 6, maximal breadth. B, upper; 2, occlusal length; 3, occlusal length of the protocone; 4, occlusal breadth.

Table 1). The dental morphological characters are shown in Text-fig. 5. All teeth and bone measurements are taken in millimetres. Since this analysis requires that no OTU has missing values, and only a few bones were complete, it was virtually impossible to obtain a large data set. No effort was made to separate males and females because, in horses, the differences in size and proportions between the sexes are lost within the general intraspecific variation (Winans 1989). With respect to this, Eisenmann (1979a) analysed the morphometric variation of the metapodials of living horses and concluded that the coefficient of variation shows a low value for all variables, except for variable #9 in MCIII, #8 and #9 in MTIII (Text-fig. 3). These few variabilities indicate low levels of dimorphism.

In long bones we have also taken the slenderness index (1)

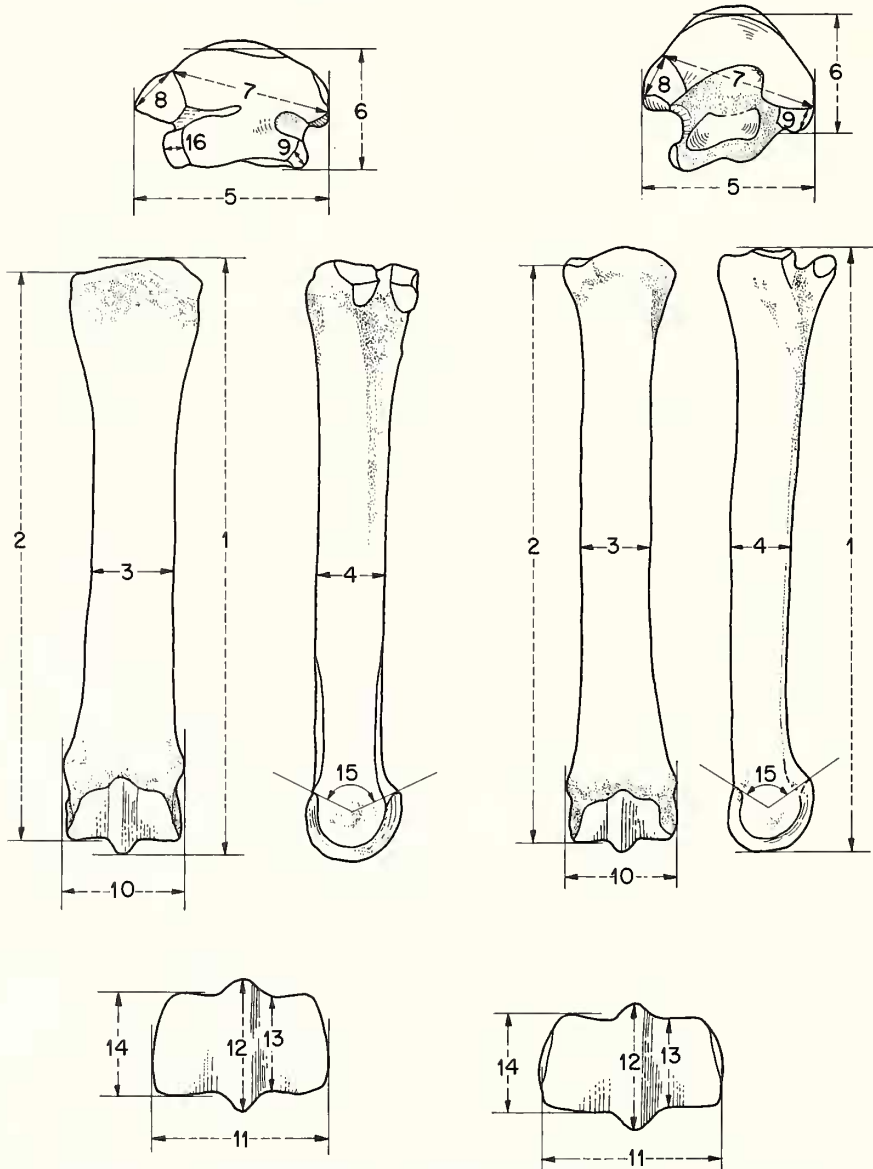
$$(1) \text{ Slenderness Index (SI)} = \frac{\text{Minimal breadth (3)} \times 100}{\text{Maximal length (1)}}$$

which serves as an indicator of the habitat where they live (more open or more wooded, harder or softer ground, etc).

A total of 26 upper dental rows, 20 lower dental rows, 49 MCIII, 35 CA, 44 AS, 61 MTIII and 101 1FALIII have been used to establish the taxonomical structure (Appendix I). The computational

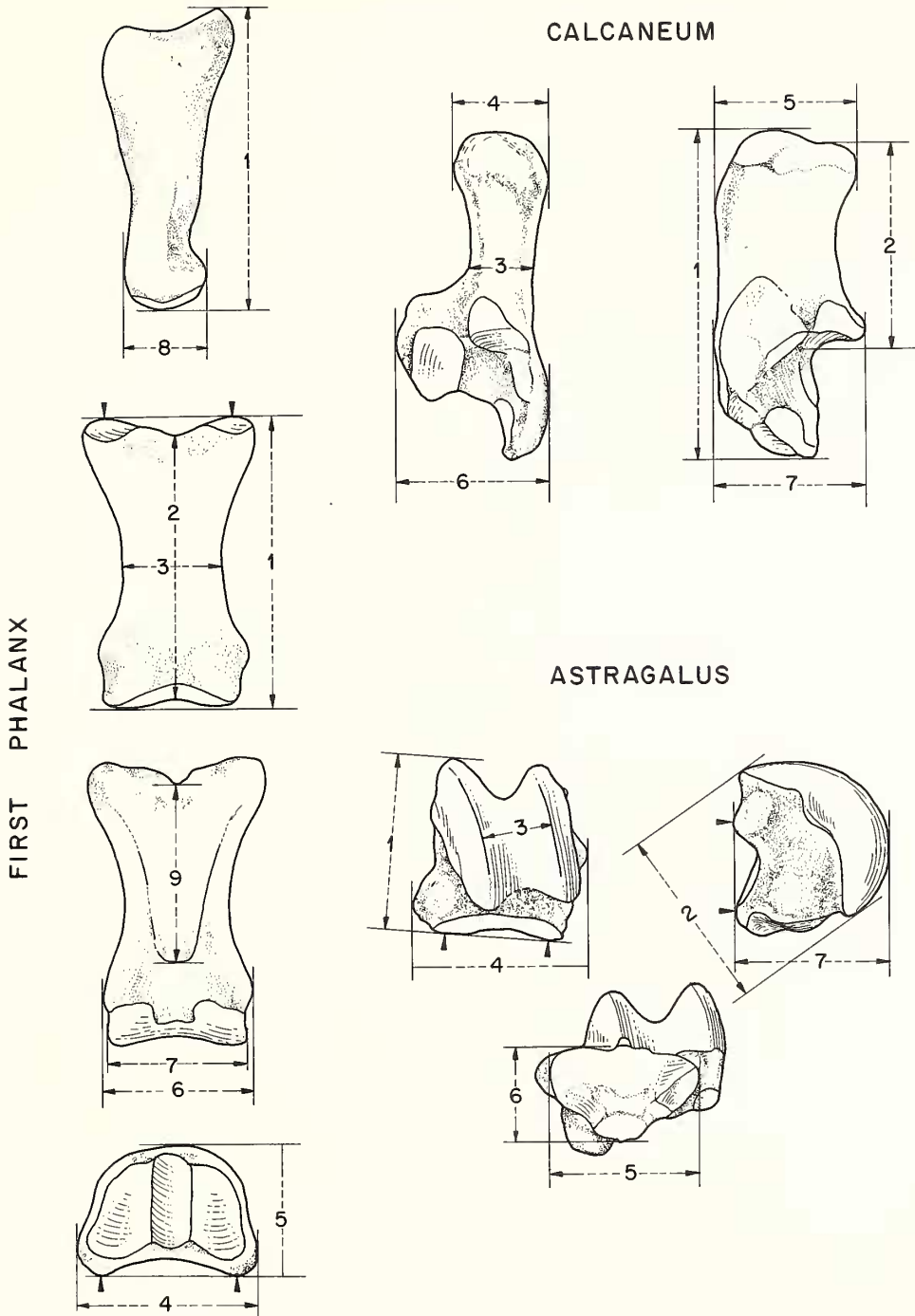
THIRD METACARPAL

THIRD METATARSAL



TEXT-FIG. 3. The measurements of the third metacarpal and third metatarsal.

work was done at the Laboratorio de Sistemática y Biología Evolutiva (LASBE) of the Museo de La Plata, using NTSYS-PC programs, version 1.60 (Rohlf 1991) and Statgraphic version 5.0 (1991). Data were analysed by three methods: cluster analysis, principal components analysis (PCA) and discriminant analysis (DA). Further details of these methods and computational procedures are in Sneath and Sokal (1973), Rohlf and Bookstein (1990) and Reyment (1991). Character-by-character correlation was obtained from each matrix by calculating the Pearson product-moment correlation coefficient between each pair of characters in each set. These matrices served as input in the PCA. The PCA was performed on each character-by-character correlation matrix and the first



TEXT-FIG. 4. The measurements of the calcaneum, astragalus and first phalanx of the third digit.

TABLE 1. The measurements of the limb bones as characteristics.

Measurements taken on third metacarpal and metatarsal

- 1 Maximal length
- 2 Medial length
- 3 Minimal breadth (near the middle of the bone)
- 4 Depth of the diaphysis at level of 3
- 5 Proximal articular breadth
- 6 Proximal articular depth
- 7 Maximal diameter of articular facet for the third carpal or tarsal
- 8 Diameter of the anterior facet for the fourth carpal or tarsal
- 9 Diameter of the anterior facet for the second carpal or tarsal
- 10 Distal maximal supra-articular breadth
- 11 Distal maximal articular breadth
- 12 Distal maximal depth of the keel
- 13 Distal minimal depth of the lateral condyle
- 14 Distal maximal depth of the median condyle
- 15 Angle subtended by condyle ends at centre of distal articulation
- 16 Diameter of the posterior facet for the fourth carpal

Measurements taken on calcaneum

- 1 Maximal length
- 2 Length of the proximal part
- 3 Minimal breadth
- 4 Proximal maximal breadth
- 5 Proximal maximal depth
- 6 Distal maximal breadth
- 7 Distal maximal depth

Measurements taken on astragalus

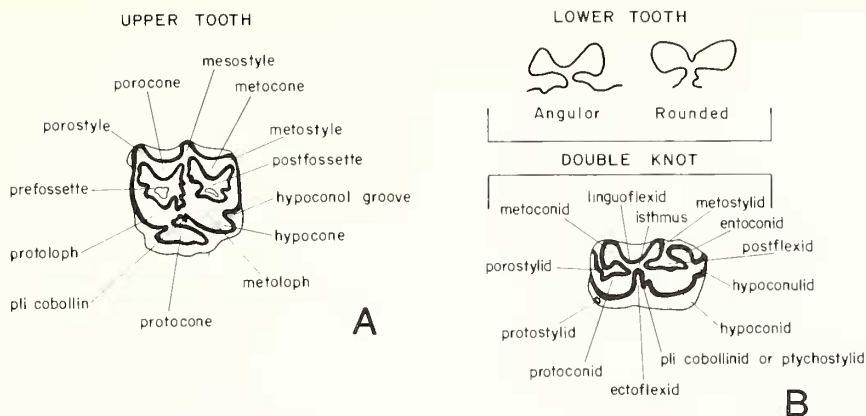
- 1 Maximal length
- 2 Maximal diameter of the medial condyle
- 3 Breadth of the trochlea (at the apex of each condyle)
- 4 Maximal breadth
- 5 Distal articular breadth
- 6 Distal articular depth
- 7 Maximal medial depth

Measurements taken on first phalanx

- 1 Maximal length
- 2 Anterior length
- 3 Minimal breadth
- 4 Proximal breadth
- 5 Proximal depth
- 6 Distal breadth at the tuberosities
- 7 Distal articular breadth
- 8 Distal articular depth
- 9 Minimal length of the trigonum phalangis

three factors were extracted. The character factor loadings were used to calculate the operational unit factor scores, or projections, in the two factor spaces. To examine ordination efficiency, the Euclidean distances between all pairs of operational units in factor space were calculated, and with the resulting matrix the cophenetic correlation coefficient was used.

After groups were identified based on examination of the PCA, discriminant analysis was used to establish a rule to differentiate these groups. DA, like PCA, is a linear function of the original variable weighted by coefficient. DA also performs a rotation of the coordinate axes, but the aim



TEXT-FIG. 5. Morphological characters of A, the upper, and B, lower cheek teeth.

was to arrive at an orientation that maximized the separation between the identified groups. DA can also be used to evaluate whether the centroids differ significantly or not, and often to identify specimens not included in the original analysis which established the groups (Marcus 1990; Reyment 1991).

In order to identify which character provided the best group discrimination, we chose the characters that showed maximal contribution values for the PCA (Table 2). To recognize the

TABLE 2. Characters that are most important for the Principal Component Analysis (PCA).

Principal component of limb bones	Number of character	Eigen value	Principal component of limb bones	Number of character	Eigen value	
Third metacarpal	First	11	Second	3	-0.566	
		4		1	0.213	
		10		2	0.209	
		5		Third metatarsal	11	0.960
		1			12	0.957
16	13	0.955				
Second	Second	8	5	0.947		
		14	14	0.946		
		6	8	-0.814		
		7	9	-0.675		
		Astragalus	First	1	1	0.190
2	2			0.190		
7	5			-0.164		
Second	First phalanx			3	6	0.969
				5	4	0.960
		4	1	0.957		
Calcaneum	First	1	Second	9	-0.400	
		6		8	-0.375	
		2		2	-0.319	

correlation character in each set of bones we undertook cluster analysis. The five character correlation matrices (MCIII, CA, AS, MTIII and 1FALIII) served as input in the calculation of a phenogram by the unweighted pair group method, using arithmetical averages (UPGMA). The cophenetic correlation coefficient (r) was computed as a measurement of distortion (Farris 1969).

RESULTS

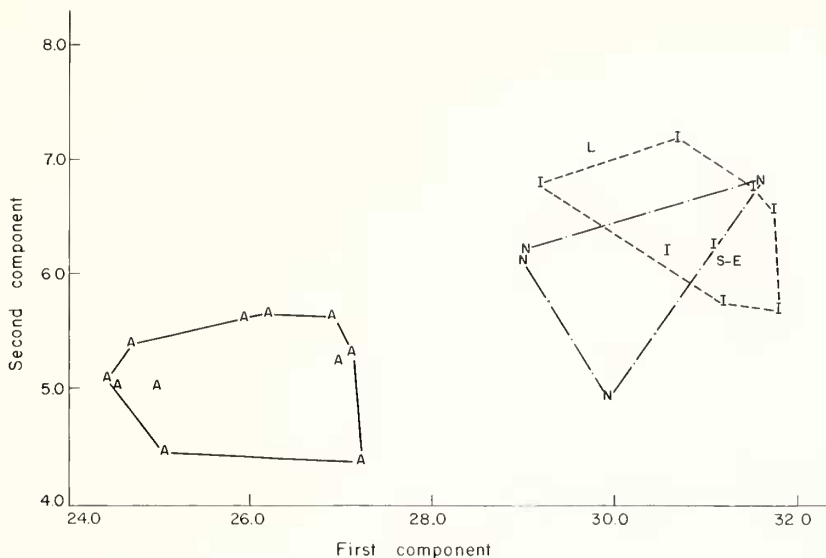
Principal component analysis, based on upper and lower dentition data, permits us to identify two main groups. The first group includes specimens of *E. andium*, the second group includes specimens referred to *E. insulatus*, *E. neogeus*, *E. santaeleuae* and *E. lasallei* (Text-figs 6–7). *E. andium* is a clear morphotype characterized by its small size adapted to mountain habitat, and can also be distinguished from the others by skeletal elements (Text-figs 8–12). The second component permits us to separate *E. lasallei* and *E. santaeleuae* and *E. insulatus* and *E. neogeus* by the occlusal breadth of the lower cheek teeth (Text-figs 2, 7). It is important to note that differences between the various species of *Equus* from South America are more evident among skeletal elements than cranial. Moreover, differences between South American horses vary more in size than in shape, consequently, the second component in the multivariate analysis plays a secondary role (see Table 2). The other group of species shows overlapping morphological patterns. For example, *E. insulatus* is an intermediate form in size between *E. andium* and *E. neogeus*, mainly for MCIII and MTIII (Text-figs 8–11). *E. neogeus*, from the Pampean region and several Brazilian localities, is the largest form in this analysis. This species is differentiated from *E. santaeleuae* by MCIII and MTIII (Text-figs 8, 11). On the other hand, *E. santaeleuae* has a 1FALIII similar to *E. neogeus* and MTIII close to *E. insulatus* (Text-figs 11–12).

E. lasallei is known only from one skull which is close to *E. neogeus* in morphological characteristics but bigger. The analysis of dentition shows little difference between them, particularly in the occlusal breadth of the lower teeth. As we do not have skeletal elements of *E. lasallei*, it is very difficult to invalidate this species.

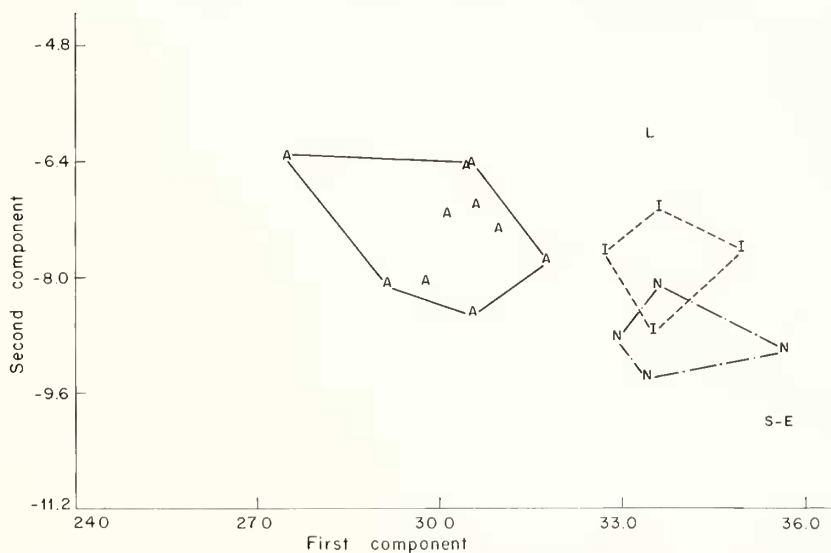
We only have two specimens of *E. martinei* from Ecuador, one MTIII and one 1FALIII, that coincide with *E. insulatus* in PCA (Text-figs 11–12).

Discriminant analysis based on all species provide a correct identification for five groups (Text-figs 15–19), especially from the upper and lower dentitions (Text-figs 13–14). DA based on MTIII and 1FALIII does not permit recognition as a group of the material comprising *E. martinei* (Text-figs 18–19). Using DA on astragalus, we observed a good discrimination of the variables. They show an overlap between *E. insulatus* and *E. andium* (weight < 4 per cent) and between *E. santaeleuae* and *E. insulatus* (weight < 13 per cent), while *E. santaeleuae* has a good discrimination (100 per cent; see Text-figure 16). From the multivariate analysis we deduce that the most characteristic features for this discrimination are: the occlusal length of the dental specimens and occlusal breadth of lower cheek teeth (2 and 6 in Text-fig. 2); the maximal breadths (5, 11) and all the distal maximal depths (12, 13, 14) of the MTIII; the maximal length (1), minimal depth of the diaphysis (4) and maximal breadths (5, 10, 11) of the MCIII; the maximal breadths (4, 6) plus maximal length (1) of the 1FALIII (see Text-figs 3–4). It is interesting to note that most of these dimensions (all breadths and some lengths) are, in general, closely related with the nature of the terrain (see Conclusions).

The cluster analysis in Text-figure 20 represents correlations between the different sets of characters (MCIII, CA, AS, MTIII and 1FALIII). In the MCIII cluster, the maximal lengths (1, 2) and the distal maximal breadths (10, 11) are highly correlated. From a functional morphological point of view this is important because it has not only taxonomic but also biological significance. The variations of dimensions 1 and 2 are directly related to the type of ground surface where these horses live (lengthening of metapodials on harder ground surfaces and shortening of metapodials on softer ground surfaces), and the variations of dimensions 10 and 11 are related with shift of weight and gait of the animal (Sondaar 1968; Hussain 1975). In the CA cluster, the maximal lengths (1, 2) are highly correlated, while in the AS cluster the maximal length (1) and the maximal diameter of the condyle (2) are also highly correlated. The variations of the dimensions 1 and 2 of the AS are

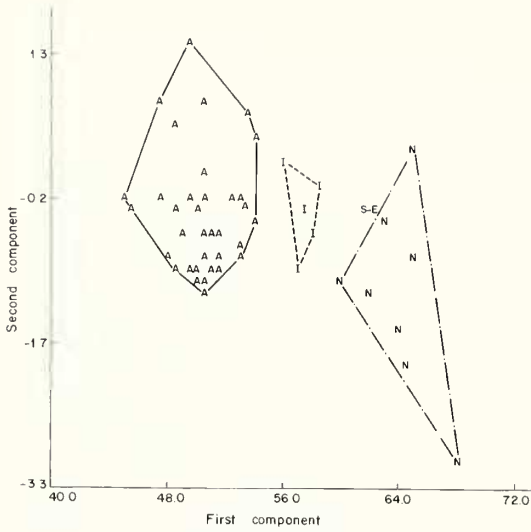


TEXT-FIG. 6. Principal Component Analysis (PCA) of the upper cheek teeth. Abbreviations: A, *Equus (Amerhippus) andium*; I, *Equus (Amerhippus) insulatus*; N, *Equus (Amerhippus) neogeus*; S-E, *Equus (Amerhippus) santacelenae*; L, *Equus (Amerhippus) lasallei*.

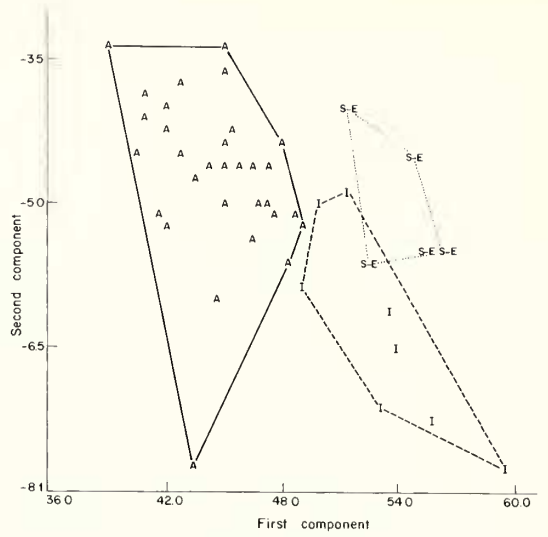


TEXT-FIG. 7. Principal Component Analysis of the lower cheek teeth. Abbreviations as in Text-figure 6.

directly related to their function. The astragalus plays an important role, as a pulley, in the forward and backward movement of the animal, since it receives the pressure of the body-weight and transmits it to the digits. Furthermore, the variation of dimension 2 of the astragalus has great implications in gait and speed of the horses. These functions are in turn controlled by dimensions 1 and 2 of the calcaneum, which contain the insertion points of the strong muscles that contribute to the same movement. For the MTIII cluster, the highest correlated characters are the lengths (1, 2), proximal breadths (5, 7) and the distal depths (12, 13). For the 1FALIII cluster these are the maximal lengths (1, 2) and the proximal and distal maximal breadths (4, 6). The variations of these



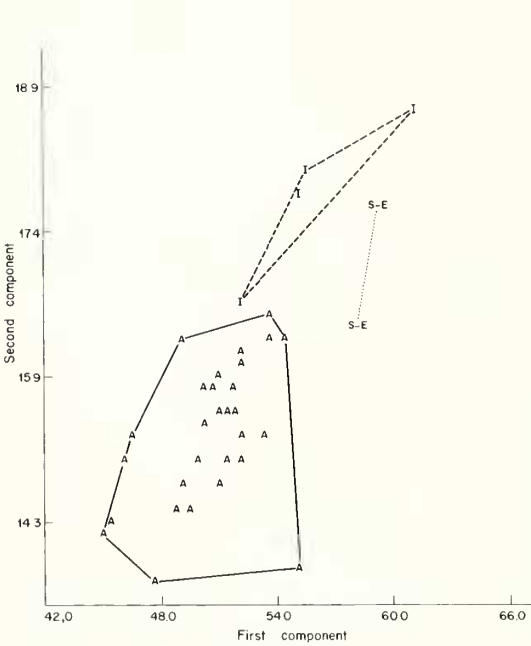
TEXT-FIG. 8



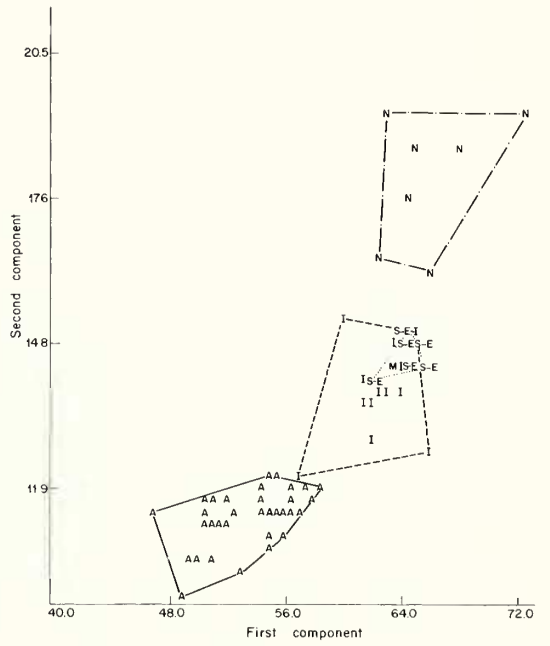
TEXT-FIG. 9

TEXT-FIG. 8. Principal Component Analysis of the third metacarpal. Abbreviations as in Text-figure 6.

TEXT-FIG. 9. Principal Component Analysis of the astragalus. Abbreviations as in Text-figure 6.



TEXT-FIG. 10

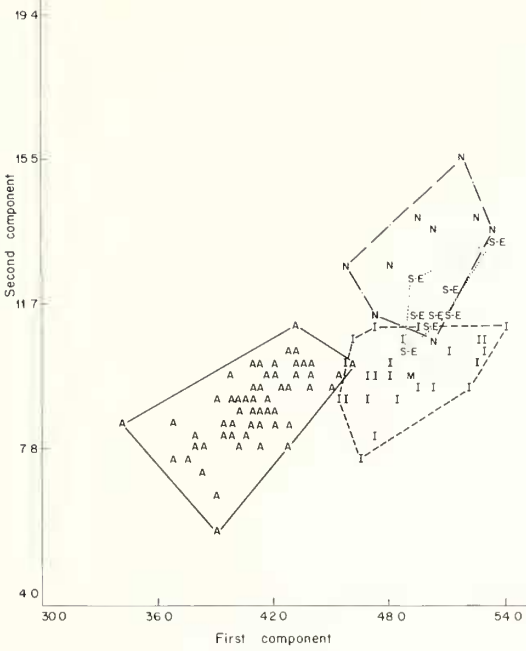


TEXT-FIG. 11

TEXT-FIG. 10. Principal Component Analysis of the calcaneum. Abbreviations as in Text-figure 6.

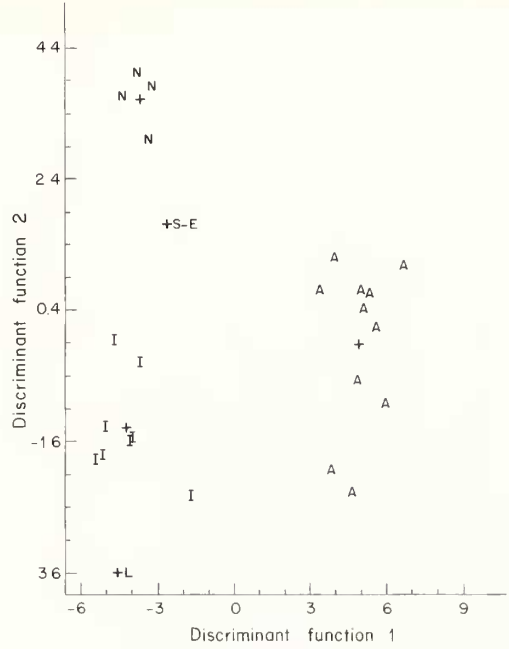
TEXT-FIG. 11. Principal Component Analysis of the third metatarsal. Abbreviations as in Text-figure 6.

M. E. (A.) martinei.



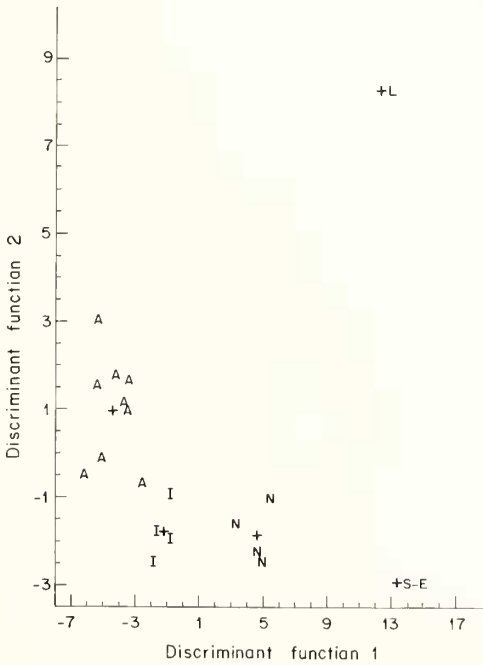
TEXT-FIG. 12

TEXT-FIG. 12. Principal Component Analysis of the first phalanx of the third digit. Abbreviations as in Text-figure 6. M, E. (*A. martinei*).



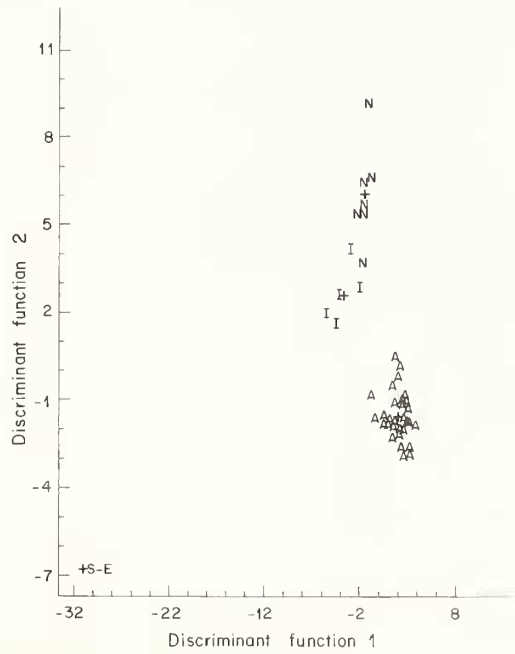
TEXT-FIG. 13

TEXT-FIG. 13. Discriminant Analysis (DA) of the upper cheek teeth. Abbreviations as in Text-figure 6. +, mean average.



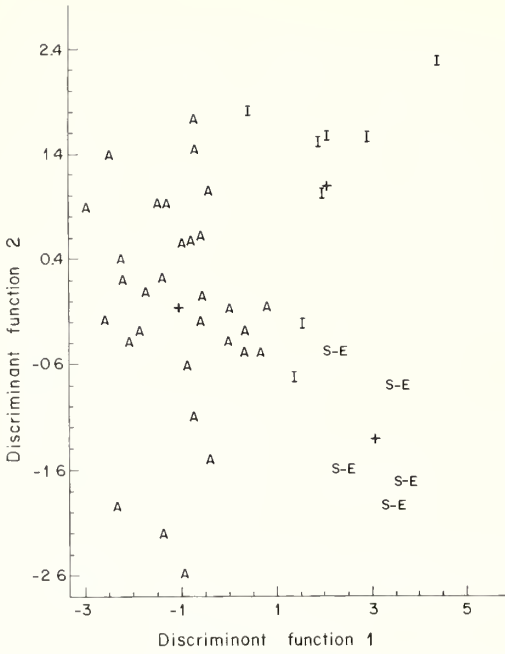
TEXT-FIG. 14

TEXT-FIG. 14. Discriminant Analysis of the lower cheek teeth. Abbreviations as in Text-figures 6 and 13.



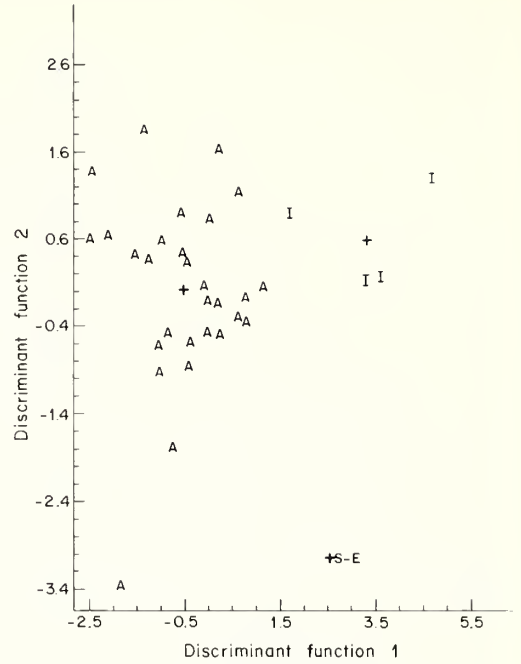
TEXT-FIG. 15

TEXT-FIG. 15. Discriminant Analysis of the third metacarpal. Abbreviations as in Text-figures 6 and 13.



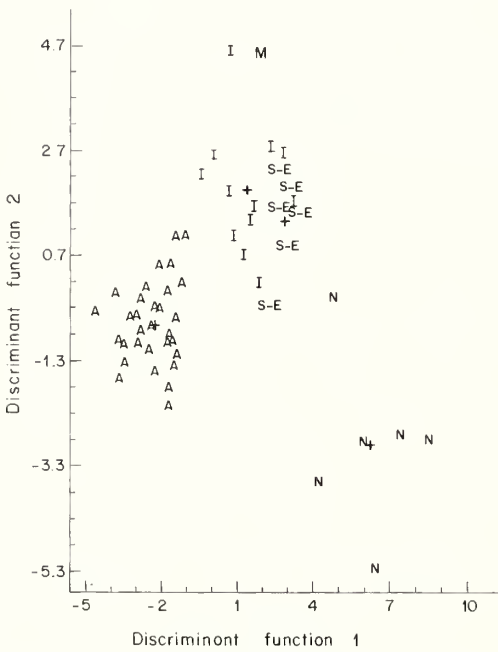
TEXT-FIG. 16.

TEXT-FIG. 16. Discriminant Analysis of the astragalus. Abbreviations as in Text-figures 6 and 13.



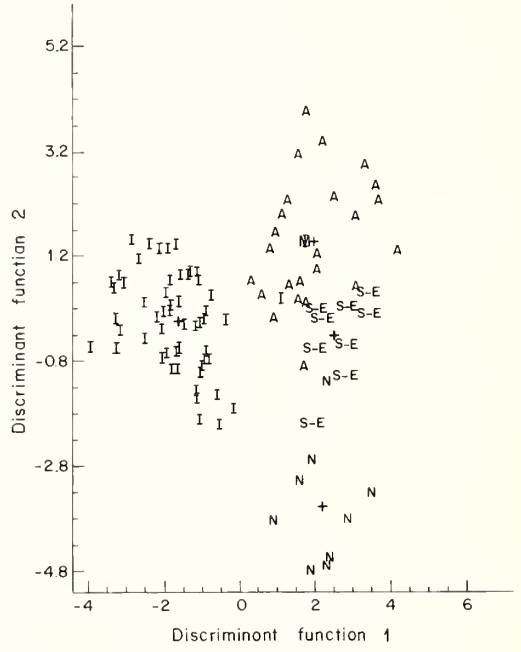
TEXT-FIG. 17

TEXT-FIG. 17. Discriminant Analysis of the calcaneum. Abbreviations as in Text-figures 6 and 13.



TEXT-FIG. 18

TEXT-FIG. 18. Discriminant Analysis of the third metatarsal. Abbreviations as in Text-figures 6 and 13. M, *E. (A.) martinei*.



TEXT-FIG. 19

TEXT-FIG. 19. Discriminant Analysis of the first phalanx of the third digit. Abbreviations as in Text-figures 6 and 13. M: *E. (A.) martinei*.

dimensions in the MTIII as well as IFALIII have a biological significance similar to that outlined for MCIII, as they reflect the skeletal modifications due to adaptation to the environment. The IFALIII represent an intermediate link in the type of movement and shift of weight of the horse.

SYSTEMATIC PALAEOONTOLOGY

Recent papers on the Equidae in South America (Alberdi 1987; Alberdi and Prado 1989, 1992, 1993) recognize two main groups: equidiforms and hippidiforms. In general, both groups show common features, possibly as a consequence of convergence due to their adaptation to similar environments: (a) large skull in relation to body size where each group has a particular dental morphology, with a certain interspecific variability; (b) a large degree of cranial flexion (Bennett 1980); (c) ventral separation of the occipital condyles; (d) robust body structure to different degrees in the different forms. The forms are heavy and not well adapted to running.

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1821

Subfamily EQUINAE (Gray 1821) Steinmann and Döderlein, 1890

Genus *EQUUS* Linnaeus, 1758

Subgenus *EQUUS* (*AMERHIPPIUS*) Hoffstetter, 1950

Synonymy (after Hoffstetter 1952, p. 233): = *Equus* (*partim*) *auct.*; = *Neohippus* (*partim*) Abel 1913, 1914, 1919; Spillmann 1931, 1938; = *Hippidiunu* Spillman 1931, *non Hippidiunu* Burmeister 1875, *nec Hippidion* Owen 1869; = *Amerlippus* Hoffstetter, 1950.

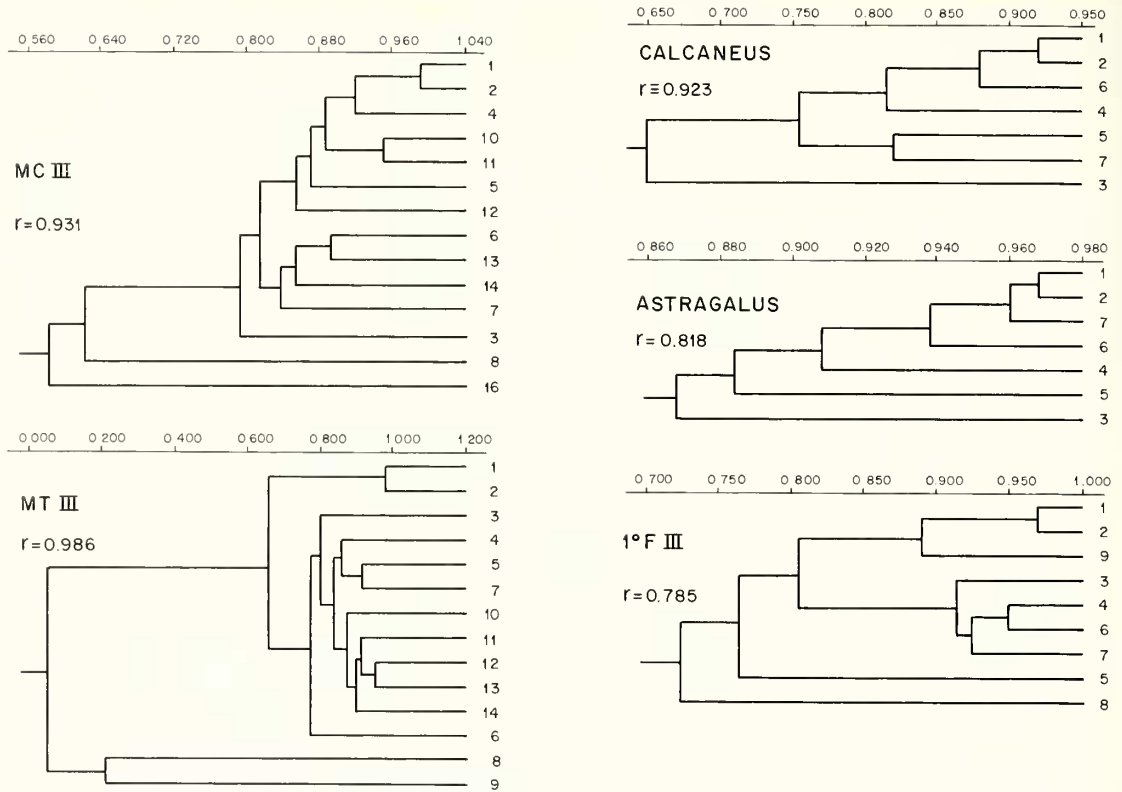
Type-species. *Equus* (*Amerhippus*) *andium* Branco, 1883, ex Wagner, 1860.

Geographical distribution. South America.

Stratigraphical distribution. *Equus* (*Amerhippus*) remains come from different levels of the South American Pleistocene, mostly from the Ensenadan and Lujanian Land Mammal Ages (Text-fig 21).

Diagnosis. *Equus* (*Amerhippus*) has a large skull with sharp and marked supraoccipital crest. It is large in relation to the postcranial skeleton, and shows a narrow and lightly excavated preorbital and nasal region. In general, there is a ventral separation of the occipital condyles but sometimes they are joined. It has a peculiar vomer disposition, which reaches the palatal processes of the maxillary anterior to the palatine. The upper cheek teeth have triangular protocones. The protocone shows the distal part longer than the mesial one, and in some cases there are enamel wrinkles. Pre- and postfossettes in the upper cheek teeth have developed folds (see Text-fig. 5A). The mandible is robust and the double-knot in the lower teeth, the metaconid-metastylid, is rounded and angular respectively. The linguaflexid is, in general, shallow and more angular in P3–P4 and more open in M1–M2. The ectoflexid varies from deep to shallow and never connects with the linguaflexid (Text-fig. 5B). The appendicular skeleton shows a shortening of the distal part of the extremities, but not as much as the *Hippidion*, and a more accentuated metatarsal distal flexion. In general, all species have robust metapodials and the SI varies within the limits for robustness of this subgenus.

Discussion. Hoffstetter (1950 p. 433; 1952 p. 245) justified this subgenus, based on only one characteristic: lack of infundibular marks in the lower incisor surface and consequent loss of surface enamel. Nevertheless, Eisenmann (1979b) analysed the first characteristic in living and fossil equids, and concluded that they show a high variability. In our opinion, this is a very variable feature because it is linked to the changes of the dental occlusal surfaces (Alberdi 1974). Consequently, its systematic value is difficult to evaluate. Notwithstanding, we think it is correct to use the subgenus



TEXT-FIG. 20. Cluster Analysis of each set of characters: third metacarpal, astragalus, calcaneum, third metatarsal and first phalanx of the third digit.

Amerhippus for different South American species of *Equus*, because all groups show the same dental morphology with a peculiarly large skull in relation to body structure, which in turn is characterized by shortness and robustness of the extremities.

Hoffstetter (1952) thought the cubitus to be stronger in South American horses than in other *Equus* and, in general, is also stronger in all similar *Equus* forms up to the present except *E. andium* due to its small size, but this is not so clear.

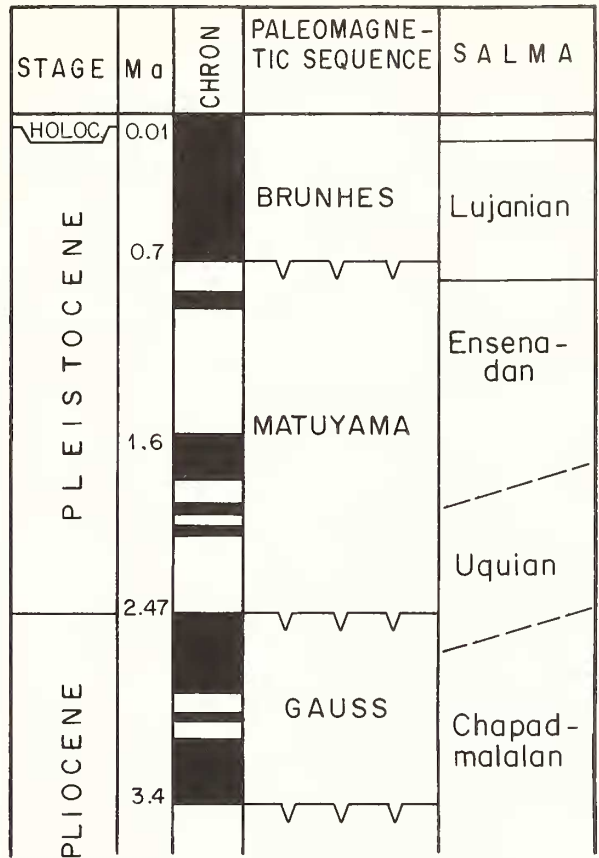
The multivariate analysis permits us to distinguish five different groups of *E. (Amerhippus)*, which we ascribe to different species.

Equus (Amerhippus) andium Branco, 1883 ex Wagner 1860

- 1860 *Equus fossilis andium* Wagner, p. 336. [nomen nudum after Mones (1986)].
- 1875 *Equus quitensis* Wolf, p. 155. [nomen nudum after Mones (1986)].
- 1931 *Hippidium jijoni* Spillmann, p. 50.
- 1938 *Neohippus rivadeneira* Spillmann, p. 386, fig. 1C.
- 1938 *Neohippus postremus* Spillman, p. 389, fig. 1E.
- 1992 *Equus andium* Branco 1883; nec Wagner-Branco Azzaroli p. 134, fig. 3b.

Type material. Hoffstetter (1952, p. 247) stated the material described by Spillmann was lost, and proposed two 'lectotypes': a specimen of *Neohippus rivadeneira* (MEPN V-78) and one of *Neohippus postremus* (MEPN V-430). We think it is best to consider the first as a neotype.

TEXT-FIG. 21. Scheme of the stratigraphical levels of Land Mammal Ages from South America (SALMA): Chapadmalalan, 'Uquian', Ensenaden and Lujanian (modified from Tonni *et al.* 1992).



Geographical distribution. From Otón, in the North, to Punín in the South of Ecuadorian Andes (Ecuador).

Stratigraphical distribution (Text-Fig. 21). The Cancagua Formation (Sauer 1965) from Ecuador; cited as Upper Pleistocene after Hoffstetter (1952), although MacFadden and Azzaroli (1987) placed it between Middle and Upper Pleistocene. Dugas (1986) described it as between 40000 and 4000 years BP and Azzaroli (1992) referred it to Late Pleistocene.

Type stratigraphical level. 'Puninian' (Hoffstetter 1952, p. 248). Lujanian Land Mammal Age.

Studied material. Material studied by Hoffstetter (1952) from several localities of the Ecuadorian Andes, stored in MEPN and IPMNH, and the material deposited in the American Museum of Natural History (Frick Collection).

Diagnosis. As for the subgenus *Amerhippus*, this species has a wide, low and laterally placed orbit. Particularly, the skeleton of *E. andium* is characterized by short and robust limbs, most significantly in the radius and metapodials, thus producing unusual proportions between these. It corresponds to a morphotype easily distinguishable from the others by the multivariate analysis of the dental and limb bones (Text-figs 6-12).

Discussion. This species has been described by Branco (1883) and Hoffstetter (1952). This form possibly presents an anatomical adaptation to environmental factors, reflected in the metapodial shortness (Mean slenderness index: MCIII = 18, 27; MTIII = 15, 81). Hoffstetter (1952) expressed doubts about this relation, considering the shortness of the extremities to be differential. This species, adapted to the Ecuadorian Andes, probably evolved from a larger form such as *E. insulatus*. It is the smallest form of *Equus* from South America.

Equus (Amerhippus) insulatus C. Ameghino, in F. Ameghino 1904

- 1851 *Equus macognathus* Weddell, p. 204.
 1855 *Equus neogaeus* Lund; Gervais, p. 33, pl. 7, figs 2–3.
 1904 *Equus insulatus* C. Ameghino [unpublished]; F. Ameghino, fig. 250.
 1938 *Neolippus martinei* Spillmann, p. 382, fig. 1b.
 1952 *Equus (Amerhippus) martinei* (Spillmann, 1938); Hoffstetter, p. 301.
 1992 *Equus martinei* Spillmann, 1938; Azzaroli, p. 137.

Holotype. MACN 1703, upper cheek teeth (M3 nor M2) figured by F. Ameghino (1904, p. 190, fig. 250). This specimen is not lost as suggested by Mones (1986).

Geographical distribution. Tarija (Bolivia), and the Ecuadorian Andes (Rio Chiche, Ecuador).

Stratigraphical distribution. (Text-fig. 21). The Tarija localities (MacFadden *et al.* 1983), and the Rio Chiche locality (Sauer 1965) are referred to the Middle Pleistocene. Hoffstetter (1952) considered *E. martinei* to be the oldest *Equus* material from Ecuador; Clapperton and Vera (1986); followed by Azzaroli (1992), assigned this locality to the Late Pleistocene.

Type stratigraphical level. Ensenadan Land Mammal Age.

Studied material. Includes material studied by Boule and Thevenin (1920) and MacFadden and Azzaroli (1987) from Tarija (Bolivia) and that from Rio Chiche, Ecuador (Hoffstetter 1952).

Diagnosis. This species has a bigger skull than *Equus (Amerhippus) andium*, but is similar in general morphology. Prominent cranial flexion between face and braincase. Nuchal crest extends posterior to occipital condyles. External auditory meatus located close to glenoid fossa. The preorbital region is also narrow but less excavated. Mandible deep and massive. Upper dental pattern characteristic of *Equus* but larger in size. Protocones moderately elongated and fossettes moderately plicated. Ectoflexids relatively shallow in the premolars and relatively deep in molars. The body size is intermediate between *E. (A.) andium* and the other species studied here (see Boule and Thevenin 1920).

Discussion. Limb bones correspond to a robust horse, with slenderness index of metapodials: MCIII = 18,16; MTIII = 16,01. *E. insulatus*, from Tarija, is similar in skull size to *E. neogens* from Buenos Aires province, however it differs from *E. neogens* in that it has dolichocephalic skull and a relatively high and narrow rostrum. The multivariate analysis permits a clear discrimination of this species from the others. The scarce specimens assigned to *E. (A.) martinei* by Spillmann (1938) and Hoffstetter (1952) are reminiscent of *E. curvidens*, but they have different skeletal proportions. We think they can be ascribed to *E. (A.) insulatus* (Text-figs 11–12) by the multivariate analysis and the morphological characters. DA also confirm this determination. The stratigraphical distribution of *E. (A.) insulatus*, classically considered as Middle Pleistocene, possibly extends to the Late Pleistocene according to some authors.

Equus (Amerhippus) neogens Lund, 1840

- 1840 *Equus neogens* Lund, p. 319.
 1840 *Equus*; Owen, p. 108, pl. 32, figs 13–14.
 1845 *Equus curvidens*; Owen, p. 235.
 1875 *Equus argentinus* Burmeister, p. 55, p. 4, fig. 6.
 1880 *Equus rectidens* Gervais and Ameghino, p. 92.
 1881 *Equus lundii* Boas, p. 307, pls 1–2; [figs 10–20 grouped all equidiform material from the Lagoa Santa].
 1905 *Equus haasei* Reche, p. 225, pl. 22.
 1912 *Equus neogaeus* [sic] Lund 1840; Sefve p. 138.
 1981 *Equus (Amerhippus) vandonii* Cunha, p. 5, pls 1–3.
 1987 *Equus (Amerhippus) curvidens* Owen; MacFadden and Azzaroli p. 331.

1992 *Equus curvidens* Owen; Azzaroli p. 134, fig. 1b.

1992 *Equus neogeus* Lund; Azzaroli, p. 134 [recorded as an uncertain species].

Holotype. Specimen 866, a right metacarpal III in the Peter W. Lund Collection, Zoologisk Museum, Copenhagen, Denmark.

Geographical distribution. Principal remains are from the Pampean region, Argentina (see *Studied material*) and others from Lagoa Santa (Lund 1840), Corumba (Cunha 1981), Sao Raimundo Nonato, Piaui (Guérin 1991) and Chique-Chique and Aguas do Araxa (Paula Couto 1979), in Brazil.

Stratigraphical distribution. Upper Pleistocene of Buenos Aires province, Argentina, and Brazil.

Type stratigraphical level. Lujanian Land Mammal Age.

Studied material. This includes the material studied by Sefve (1912), such as *E. neogaeus* and *E. curvidens* from Mercedes (Luján), Ayaeucho, Necochea, Río Quequén Salado, Paso Otero, Arroyo Tapalqué, Montehermoso, among others, in Buenos Aires province, dated by ¹⁴C between 28000 and 4000 years BP (Carbonari *et al.* 1992), and the material from Brazilian localities.

Diagnosis. This is one of the largest species of South American horses. The skulls are big and show an enlarged preorbital and nasal region. The limb bones are large and robust, but more slender than in the other South American *Equus* species. See the description by Sefve (1912, p. 138).

Discussion. The multivariate analysis both distinguishes this species from the rest (Text-figs 8, 11–12), and groups together all specimens from the Buenos Aires province sites, and the Brazilian localities. They are slenderer (MCIII = 16, 16; MTIII = 12, 33). Sefve (1912) thought it very difficult to separate this species, if its dimensions are not considered, and explained that *E. neogeus* is both the biggest and the most slender South American *Equus*. Winge (1906) synonymized *E. neogeus* with *E. curvidens*, but we consider that priority belongs to *E. neogeus*.

From the nomenclatorial point of view, Lund (1840) described *E. neogaeus* from a metatarsal III found at Lagoa Santa; in 1846, he described new remains from the same place. He referred two molars to *E. neogaeus*, one molar to *E. principalis* and the rest to *E. aff. caballus*. Gervais (1855) assigned part of this material to *E. neogaeus* and part to *E. devillei*. Owen (1869) erected *Hippidion*, which in 1870 included *E. neogaeus*, *E. principalis* and *E. arcidens*. Boas (1881) considered that the metatarsal described by Lund (1840), to be a metacarpal, and therefore he created a new species, *E. lundii*; the molars referred by Lund (1846) as *E. aff. caballus* were considered conspecific. Winge (1906) considered all material from Lagoa Santa as *E. curvidens*. Sefve (1912) referred to *E. neogaeus* as all the material from Lagoa Santa and to *E. curvidens* as the material from the Pampean region. In 1971, Cunha summarized these references thoroughly and explained that only the teeth referred by Lund (1846) to *E. neogaeus* and *E. principalis*, correspond to *Hippidion*, while the metacarpal and remaining teeth correspond to *Equus*.

Owen (1840) mentioned and figured one horse which he later (1845) named *E. curvidens*. Based on the rules of Principle of Priority (ICZN, 1985), we consider *Equus neogeus* (not *neogaeus*) should have priority over *E. curvidens*.

Equus (Amerhippus) santaeelenae (Spillmann, 1938)

1938 *Neohippus santae-elenae* Spillmann, p. 384, fig. 1D.

Neotype. MEPN V-3037, partial skull of an adult male, Hoffstetter (1952 fig. 85A). The skull figured and photographed by Azzaroli (1992 p. 138, text-figs 1d and 2 is specimen V-3037, not V-68).

Paratypes. V-1, V-3, V-5–V-6, V-10, V-12, V-18, V-20, V-23, V-25–V-30, V-35, V-37, V-40, V-44, V-52, V-59, V-63, V-65, V-68–V-69, V-175–V-180, V-182–V-183, V-187, V-191, V-192, V-215–V-216, V-224, V-242, V-1402–V-1404, V-1407, V-1457, V-1460–V-1462, V-3798.

Geographical distribution. La Carolina and Salinas Oil Fields localities in Santa Elena peninsula (Ecuador).

Stratigraphical distribution. Upper Pleistocene. Material was recovered from Pichilingue Formation, dated by ^{14}C as 26000 ± 100 BP (Baldock 1982).

Type stratigraphical level. Lujanian Land Mammal Age.

Studied material. Material from the Frick collection, [AMNH]; material studied by Spillmann (1938) and Hoffstetter (1952) from MEPN and MNHN.

Comparative diagnosis. Mandible robust similar to the other species of *E.* (*Amerhippus*) and with more posterior position of the canine. The molars are proportionately wider in relation to their length. In the upper cheek teeth, the enamel is more wrinkled than in *E. andium*, while in the lower cheek teeth, the wrinkling is more complex. The postcranial skeleton is larger and stronger than in *E. andium*, but similar in morphology despite living in a different environment. The shortening of the length of the radius and metapodials are also similar to those observed in *E. andium*. However, *E. santaeelenae*, has a wider and heavier skeleton: see Spillmann (1938, p. 384) and Hoffstetter (1952, p. 288).

Discussion. The skull fragment is similar to *Equus* (*Amerhippus*) *neogeus*, but smaller. The protocone is longer, elongated at the distal part, with a certain enamel complication and the lingual groove very marked (Hoffstetter 1952, pp. 288–301). Only the multivariate analysis of lower dentition shows a clear discrimination for this species (Text-fig. 7). The analysis of the postcranial bones shows that the MTIII and AS are like *E. insulatus* morphology (Text-figs 9 and 11), while 1FALIII overlaps *E. neogeus* (Text-fig. 12). This indicates different proportions in relation to the other forms. One particular feature in this species is the slenderness index that shows different patterns between MCIII (18,18) and MTIII (15,11). On the other hand, the similarities between *E. santaeelenae* and *E. andium* observed by Hoffstetter (1952) have not shown up in the multivariate analysis carried out by us on MCIII, CA, AS MTIII, and 1FALIII, where the studied material has been more abundant.

We think that *E. (A.) santaeelenae* shares some adaptive characters in limb bones with *E. neogeus*, but differs from it in dental morphology, especially in the protocone.

Equus (*Amerhippus*) *lasallei* Daniel, 1948

1948 *Equus lasallei* Daniel, p. 278, fig. 66.

1960 *Equus* (*Amerhippus*) *lasallei* Daniel; Porta, p. 53, figs 3–8, pls 1–2.

Holotype. MCLU, unnumbered specimen, an old skull from Cerrogorido, Colombia (Daniel, 1948). Redescribed and figured by Porta (1960, p. 53, pls 1–2).

Geographical distribution. Cerrogorido (Porta 1960) and Tibito (Correal Urrego 1981), Colombia.

Stratigraphical distribution. Late Pleistocene. Porta (1960) correlated the Cerrogorido locality with the Punian in Ecuador (*sensu* Hoffstetter 1952). The Tibito site was dated by ^{14}C as 11740 ± 110 years BP (Correal Urrego 1981).

Type stratigraphical level. Lujanian Land Mammal Age.

Studied material. A complete skull collected by Brother Daniel (Porta 1960) and a few remains from Tibito (Correal Urrego 1981) from MCLU and NUB (Colombia).

Diagnosis. The skull is high and long, with a longer diastema and relatively slender rostrum. The forelobes of the occipital condyles are joint. Upper cheek teeth contain widely developed fosses

and the enamel line is wrinkled giving a complex pattern. Lower cheek teeth are greater in breadth than in other species. See Porta (1960, p. 253).

Discussion. *Equus lasallei* has the largest skull among the South American horses. The presence of the forelobes of the occipital condyles joint is also observed in the skull described by Reche (1905) as *E. haasei*. Both skulls belong to old animals. We have observed the joint to be a variable character in some equids, and consequently we think it is possible that it may be related to the age of the animal. Unfortunately, we know only the skull of this species, which corresponds to a male, and do not yet have limb bones to permit more extensive analysis. The multivariate analysis, which was clearly taken only for dentition, shows that the lower cheek teeth produce the best discrimination (Text-fig. 7) and the breadths are the most significant character that contribute to the second component. We think this *Equus* can be considered a good species based on the skull morphology. This morphology is similar to *E. neogeus* but bigger in size. Future finds of postcranial remains could permit us to form a better definition of this species.

CONCLUSIONS

The results of the morphological study of the skull agree with those obtained from the multivariate analysis of the limbs. The conclusions can be summarized as follows:

Equus (Amerhippus) Hoffstetter (1950) arrived in South America from North America after the Great American Biotic Interchange. This subgenus has been recorded in South America from the Middle Pleistocene to the Pleistocene-Holocene boundary.

We recognize five species of *Equus (Amerhippus)* as valid: *andium* Branco, 1883, *ex* Wagner (1860); *insulatus* Ameghino, 1904; *neogeus* Lund, 1840; *santaeelenae* (Spillmann, 1938), and *lasallei* Daniel, 1948. We include as synonyms: *Equus curvidens* Owen, 1845, *E. haasei* Reche, 1905 and *E. martinei* (Spillmann, 1938) from the latest review by Azzaroli (1992).

The geographical distributions of these species are clear, without geographical overlap, from Colombia in the north to Buenos Aires province in the south.

The oldest record is *E. (A.) insulatus*, from the Middle Pleistocene of Tarija (Bolivia). The other species come from the Upper Pleistocene of different localities in Brazil, Colombia, Ecuador and Argentina. The most southern distribution corresponds to *E. neogeus* in the Pampean region.

The family Equidae is classically considered as a good biostratigraphical and palaeoecological marker based on their wide record in the Northern Hemisphere. The South American equids reflect the last step of this evolutionary lineage in a short period of time (Pliocene/Pleistocene). Nevertheless, the adaptive characteristics of the *Equus (Amerhippus)* species to different habitats can be correlated with the differences in their extremities, mainly in their distal part as observed in other *Equus* species (Gromova 1949; Eisenmann 1979a, 1979c, 1984; Eisenmann and Karchoud 1982; Eisenmann and Guérin 1984). The metapodials of *Equus*, in general, vary in relation to the type of ground, both in length and width, though without any direct relation between these dimensions. Duerst (1926) considered the degree of slenderness of the skeleton to be related to the environmental conditions. For example, he considered that robustness (short and wide metapodials) was related to a humid and cold climate in a wooded environment, while conversely, slenderness (long and narrow metapodials) was related to a warm and dry climate and open landscape. On the other hand, Gromova (1949) established a correlation between the widening of the third phalanges of the third digit and the characteristics of the ground; the largest are related to soft soils and the narrowest, to hard soils. This pattern is based on the ecology of living horses. In South America, the genus *Equus* is conservative in morphology and shows important differences in size and gracility of the distal part of the extremities, according to the environmental conditions. *E. (A.) neogeus* and *E. (A.) santaeelenae*, from the plains regions, are the largest in size; the former is more slender and comes from the open plains; the latter, stronger, comes from a restricted area with more sandy ground. *E. (A.) insulatus* and *E. (A.) andium* are intermediate forms with bigger and stronger second and fourth lateral metapodials, and show comparatively shorter metapodials than the plains forms. This

is more marked in the last species *E. andium*. We consider this character as adaptively related to a mountain habitat with hard ground and steep relief. Moreover, we think it may be considered as an adaptive convergence with the small *Hippidion* species also from South America. In general, we observed a similar structure in both *Hippidion* and *Equus* genera from South America that may indicate an adaptive convergence to the environment. In work in progress we are attempting to determine the relation between body size and weight of Equidae from different continents.

We conserve the validity of name *E. (A.) lasallei* for the Cerrogorido (Colombia) specimens while awaiting further evidence of the postcranial skeleton.

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APPENDIX I

*Localities of specimens included in this study grouped by species**Equus (Amerhippus) andium.*

Upper dentition: MEPN: V.2152, V.76, V.2161, V.2135, V.2163, V.374, V.381, V.403; IPMNH: V.2159; AMNH: #19, #6. *Lower dentition*: MEPN: V.2162, V.2138, V.2164, V.2132, V.2145, V.281, V.2186, V.290, V.242; IPMNH: V.2181. *MCIII*: MEPN: V.2280, V.2414, V.2408, V.2412, V.4014, V.470, V.2415, V.2411, V.466, V.2416, V.1499, V.2301, V.1505, V.2302, V.469, V.472, V.467, V.2410, V.464, V.465, V.4084, V.1501; IPMNH: 6 unnumbered specimens, Hoffstetter Col.; AMNH: EcuA.41, EcuA.42, 5 unnumbered specimens. *CA*: MEPN: V.2388, V.2229, V.2220, V.2281, V.2222, V.2231, V.2218, V.2219, V.2386, V.2216, V.517, V.4111, V.2221, V.4112, V.4114, V.2232, V.516; IPMNH: AA4/7, 1 unnumbered specimen; AMNH: 10 unnumbered specimens. *AS*: MEPN: V.2239, V.2251, V.2223, V.2249, V.2236, V.511, V.2390, V.2286, V.510, V.507, V.508, V.2248, V.2242; IPMNH: 1 unnumbered specimen, Hoffstetter Col.; AMNH: 17 unnumbered specimens. *MTIII*: MEPN: V.458, V.2417, V.2328, V.1492A, V.1489, V.1490, V.1495, V.1494, V.2222, V.1493, V.1488, V.4073, V.4076, V.456; IPMNH: 6 unnumbered specimens, Hoffstetter Col.; AMNH: 14 unnumbered specimens. *IFALIII*: MEPN: V.2352, V.474, V.2325, V.2328, V.2346, V.2343, V.2329, V.4086, V.2339, V.2336, V.2397, V.2338, V.2401, V.501, V.483, V.2334, V.2228, V.2327, V.2332, V.2341, V.2349, V.2335, V.2331, V.502, V.2330, V.477, V.481, V.2342, V.2396; IPMNH: 2 unnumbered specimens, Hoffstetter Col.; AMNH: 29 unnumbered specimens.

Equus (Amerhippus) insulatus

Upper dentition: IPMNH: TAR.996, TAR.997, TAR.783, TAR.1142; MNHN: 002160, 001432, 000922, 1 unnumbered specimen. *Lower dentition*: MNHN: 000679, 001576, 001577, 001415. *MCIII*: IPMNH: TAR.1175, TAR.1179, TAR.1176, TAR.1177, TAR.1178. *CA*: MNHN: 001296, 001293, 001298, 001297; GEOL: UF.91956. *AS*: MNHN: 001302, 001303, 001301, 001306, 001305, 001291, 001290, 001304. *MTIII*: MEPN: V.543 (*E. martinei*); IPMNH: TAR.1192, TAR.1188, TAR.1190, TAR.1182, TAR.1193; MNHN: 001020, 001029, 001031, 001028, 001032, 001018, 001019, 001010. *IFALIII*: MEPN: V.543 (*E. martinei*); MNHN: 001256, 001254, 001255, 001263, 001257, 001258, 001252, 001265, 001266, 001268, 001260, 001277, 001270, 001275, 001271, 001269, 001259, 001262, 001273, 001274, 003132, 001038, 001013, 003129.

Equus (Amerhippus) neogeus

Upper dentition: MLP: 6.1, 6.7; MACN: 1288, 11721, 1115. *Lower dentition*: MACN: 9753, 2835, 1603, 5401 (1835). *MCIII*: MLP: 85-II-10.3a, 63-VI-10.17, 6.305, 6.402 (6.412), 6.106, 6.306, 6.397, 28-III-16.8. *MTIII*: MLP: 68-IX-3.3, 85-II-10.4, 63-VI-10.17, 6.42, 6.56, 6.10; MACN: 1 unnumbered specimen. *IFALIII*: MLP: 85-II-10.3b, 85-II-13.3b, 86-III-25.17, 55-VIII-12.1.1; 6.42, 6.360, 6.219, 3 unnumbered specimens (PA-OT).

Equus (Amerhippus) santaecelenae

Upper dentition: MEPN: V.3037. *Lower dentition*: AMNH: 39409. *MCIII*: MEPN: V.37. *CA*: IPMNH: LAR.55 (V.20); AMNH: 1 unnumbered specimen. *AS*: MEPN: V.3786, V.17, V.16; IPMNH: LAR.56 (V.18); AMNH: 1 unnumbered specimen. *MTIII*: MEPN: V.35, V.31; IPMNH: LAR.48 (V.33); AMNH: 3 unnumbered specimens. *IFALIII*: MEPN: V.40, V.44, V.47, V.41, V.45, V.43; IPMNH: LAR.51 (V.42), LAR.65 (V.40).

Equus (Amerhippus) lasallei

One cranial specimen with upper and lower dentition (MCLU, unnumbered).